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Structure and Affinities of the Petrified Plants from the Cretaceous of Northern Japan and Saghalien VI. *Yezosequoia shimanukii* gen. et sp. nov., a Petrified Taxodiaceous Cone from Hokkaido

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北日本及びサハリンの白亜紀産石化植物VI スギ科球果の新属新種 *Yezosequoia shimanukii*

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Yezosequoia is a new genus of permineralized taxodiaceous cone based on three specimens from the Upper Cretaceous of Hokkaido, Japan. The type species, *Y. shimanukii* sp. nov., is characterized by peltate bract-scale complex consisting of a large bract and a small scale almost fused with each other. Each complex is fan-shaped with inverted ovules. It is anatomically comparable to *Athrotaxis* and *Sequoia,* particularly to the latter and is regarded to be one of extinct representatives of the Taxodiaceae. (Continued from Nishida, Bot. Mag. Tokyo **102**: 255–282, 1989)

Petrified coniferous cones from the Cretaceous of Japan are reported only from Hokkaido. *Cunninghamiostrobus yubariense* Stopes et Fujii (1910, Ogura 1930), is the only one species that has been described preceding to our preliminary works on fossil cones of Hokkaido (Nishida 1974, Nishida and Nishida 1979). Recently two species of Araucarian cones have been observed (Stockey, Nishida and Nishida in preparation).

In the past four years several amateur collectors in Hokkaido provided us with ten or more petrified cones, representing three taxa of pityostroboid, two of cupressoid and several of taxodiaceous affinities. Of these specimens, pityostroboid cones are being described by Ohsawa, Nishida and Nishida (in preparation). This paper is a result of the studies of taxodiaceous cones.

Several species of taxodiaceous cones other than those mentioned above from the Cretaceous have been described worldwide. They are *Sphenolepis kurriana* (Dunker) Schenk (Schenk 1871, Harris 1953), *Elatides brandtiana* Heer (1876), *E. ovalis*

Heer (1876), *E. bommeli* Harris (1953), *Cunninghamiostrobus hueberi* Miller (1975), *Austrosequoia wintonensis* Peter et Christophel (1978), *Nephrostrobus bifurcatus* La Pasha et Miller (1981), *N. cliffwoodensis* La Pasha et Miller (1981), *Rhombostrobus cliffwoodensis* La Pasha et Miller (1981) and *Athrotaxites berryi* Miller et La Pasha (1983).

Terminology

Descriptive terms used here concerning coniferous cones are after Miller (1975). Bract-scale complex, scale, and bract are for cone-scale complex, ovuliferous scale, and bract-scale of Florin (1951), respectively.

Materials and methods

Three new cone specimens, nos. 860824, 860829 and 880011 have been obtained. Since all occur in nodules, we could not examine external morphology of cones. Specimen no. 860829, provided by

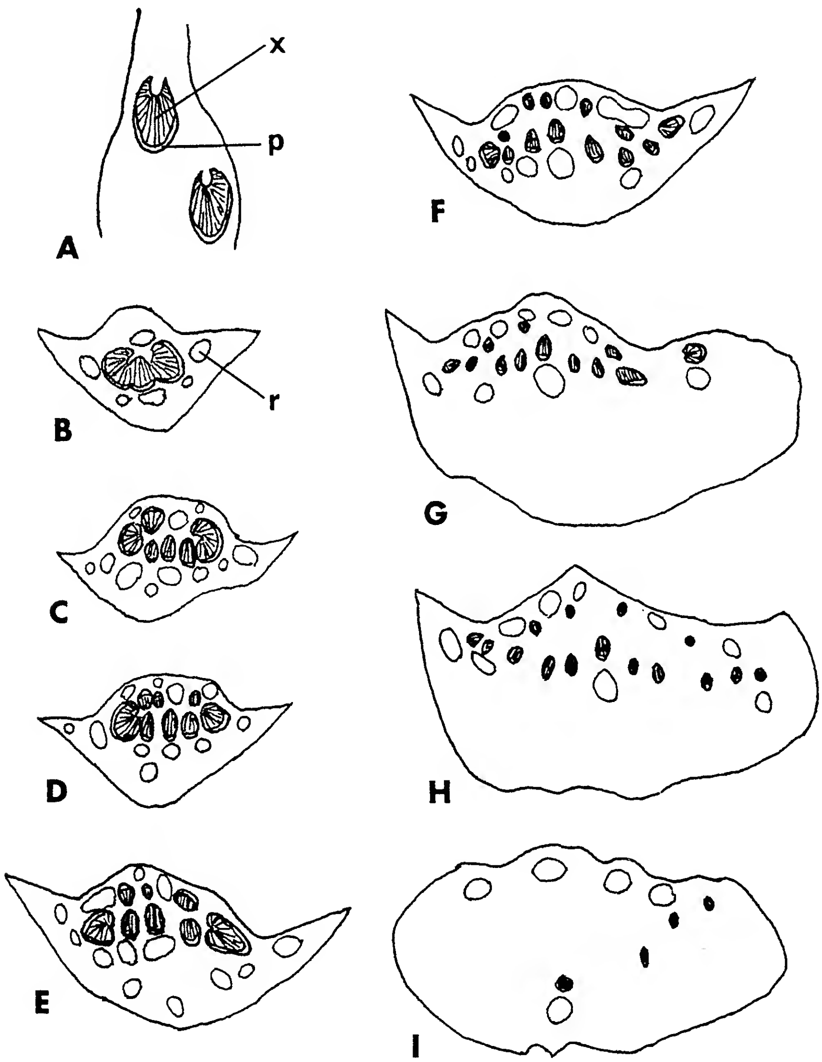

Fig. 1 Semi-diagrammatic figures of serial cross sections of bract-scale complexes of *Yezosequoia shimanukii,* showing their vasculature. p: phloem. r: resin canal. x: xylem.

Mr. Toshio Shimanuki, was collected from the riverbed of the Obirashibe-gawa River, Kawakami, Obira Town, and is fairy well preserved in histology. It was examined in longitudinal section. Specimen no. 860824, collected by Mr. Isamu Nakajima, from the same locality, is poorly preserved. Specimen no. 880011, also collected by Mr. Nakajima from the riverbed of Kumaoi-zawa, on the north side of Lake Katsura-zawa, Mikasa City, is a portion of a cone and well preserved in histology. Nodules collected at Obira are derived from the uppermost part of the Middle Yezo Group or the Upper Yezo Group, and Mikasa nodule from the Upper Yezo Group. The first two are believed to be Late Turonian to Santonian in age (Tanabe et al. 1977), and the third to be the Coniacian to Santonian (Matsumoto et al. 1976). All micropreparations used in this study were made by cellulose acetate peel technique using 0.5 N hydrochloric acid as an etching reagent.

Systematic treatment

Order Coniferales

Family Taxodiaceae

Genus *Yezosequoia* gen. nov.

Diagnosis of the genus. Fossil cone, conical, up to 29 mm long and 25 mm wide. Bract-scale complexes spiral on median axis, about 20 seen in median longisection. Scale small, completely fused with larger bract. Bract-scale complex somewhat peltate, with small spine-like projection. Pith of cone axis consisting of parenchyma cells and thick-walled sclereids. Cortex consisting of thick-walled parenchyma cells and bearing ring of resin canals. Vascular trace to bract-scale complex C-shaped in cross section, dividing in cortex to form large collateral bract traces abaxially and small collateral scale traces adaxially. Bract trace divides to form series of strands. Ground tissue of bract-scale complex consisting of fibers proximally, changing to parenchyma cells and fibers distally. Resin canals in bract abaxial to vascular strands; those in scales adaxial to strands. Seeds four per scale, inverted and with lateral wings.

Type of the genus: *Yezosequoia shimanukii* sp. nov.

Diagnosis of the species. Seed cones conical; more than 20 helically arranged bract-scale complexes present in median longisection. Scale small, completely fused with large bract. Cone axis tapering toward cone apex; pith of parenchyma cells and thick-walled sclereids; vascular tissues in continuous cylinder. Primary xylem endarch; secondary xylem tracheids with circular bordered pits on radial walls, rays uniseriate and 1–7, mostly 1–4 (85%), cells high. Secondary phloem of sieve cells and thick-walled fibers. Cortex of thick-walled parenchyma cells, with one ring of large resin canals. Vascular trace to bract-scale complex C-shaped in cross section, dividing in cortex to form large collateral bract traces abaxially and small collateral scale traces adaxially. Bract-scale complex somewhat peltate, with small spine-like projection. Bract-scale complex trace divides into 3 bundles. Lateral bundles divide to form small strands which supply scale adaxially, forming ring of bundles. Abaxial bract bundles larger in outline and greater in number than adaxial scale bundles. Bract trace divides to form series of strands. Fundamental tissue of basal part of scale composed of sclerenchyma fibers, distally changing to parenchyma cells and fibers. Resin canals in bract abaxial to vascular strands; those in scales adaxial to strands.

Type and deposition. Specimens, nos. 860824, 860829 (holotype) and 880011 are housed in the Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University.

Locality. Riverbed of the Obirashibe-gawa River, Kawakami, Obira Town, Rumoi-gun,

Hokkaido (nos. 860824 and 860829), and riverbed of Kumaoi-zawa, a branch stream of the Katsura-zawa River, Ikushumbetsu, Mikasa City, Hokkaido (no. 880011).

Horizon and Age. Uppermost part of the Middle Yezo Group and Upper Yezo Group. Coniacian-Santonian and Turonian-Santonian.

Ethymology. Generic name *Yezosequoia* is from an old name of Hokkaido, Yezo and extant genus *Sequoia*. Specific epithet is to be dedicated to Mr. T. Shimanuki, the collector of the type specimen.

Description of the species

External morphology. Cones are conical,

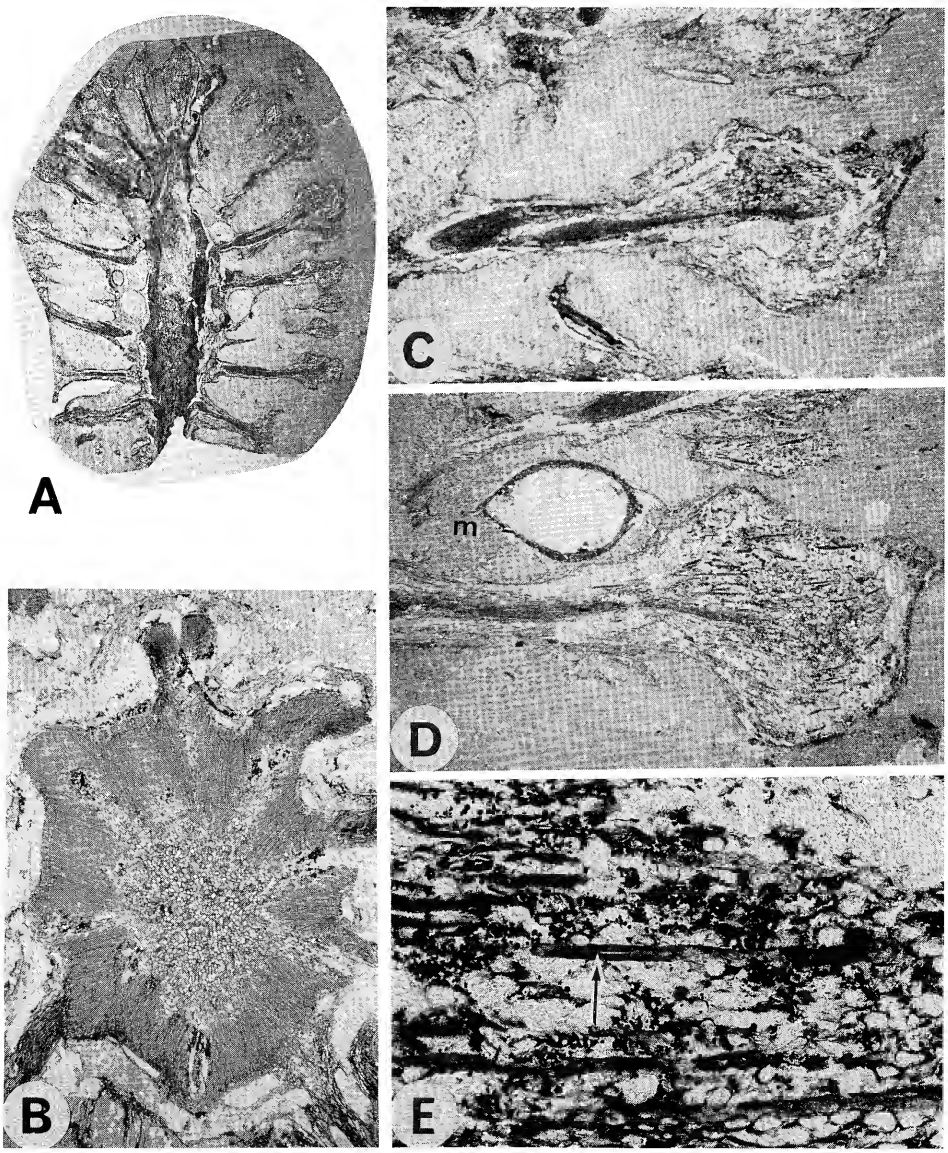

Fig. 2. *Yezosequoia shimanukii* sp. nov.
A: Median longitudinal section of a cone, B: Cross section of cone axis, C and D: Longitudinal sections of bract-scale complex showing the peltate structure with a small projection at the tip. Showing an ovule in D. E: A magnified figure of a part of D, showing sclerenchymatous fibers (arrow). m: micropylar side of the ovule. A: ×1.8. B: ×9. C: ×8. D: ×9. E: ×68.

22–29 mm long and 20–25 mm wide (Fig. 2A). The cone axis is 6–8 mm in diameter in the middle of specimens (Fig. 2B). About 20 bract-scale complexes are seen in one longisection. These are 6–9 mm long, 2.5–4.0 mm thick and 6–10 mm wide, helically arranged around the cone axis (Fig. 2A). Each consists of basal stalk portion and a distal laminar region (Fig. 2C, D). Scales and bracts are fused completely. The apical region of the bract-scale complex is cuneiform or more or less peltate with a small spine-like projection (Fig. 2C).

Cone axis. The pith is 1.1–2.0 mm in diameter and composed of thin-walled parenchyma cells and scattered small numbers of thick-walled sclereids (Fig. 2B; Fig. 3C, D). Pith cells are polygonal in cross section, 36–98 μm in diameter and 60–110 μm long near the center of the tissue and grade to cells that are 20–60 μm in diameter and 80–122 μm long at the periphery. Vascular cylinders are 0.7–1.2 mm thick at the base of the cone axis and consist mostly of secondary xylem which is interrupted by only radially diverging traces to bract-scale complexes (Fig. 2B). Endarch primary xylem strands are visible in places at the inner edge of the vascular cylinder (Fig. 3A). They are 7–10 in number. The tracheids are round to polygonal in cross section, 10–20 μm in diameter; there is no evidence of a growth ring (Fig. 3A; Fig. 4A). Bordered pits on radial walls of the tracheids are 8–10 μm in diameter and arranged separately in a single row (Fig. 5E). Rays are sparse, uniseriate, 1–7, mostly 1–4 (85%), rarely up to 11 cells high, or 24–197 μm in height (Fig. 5D). Ray cells are ovoid or rectangular in tangential section, 19–34 μm in vertical and 12–17 μm in transverse widths. One or two circular, 3.5–4.8 μm in diameter, pits occur in the cross field (Fig. 5E). Secondary phloem is 120–160 μm thick and poorly preserved (Fig. 3C, E). The cortex, about 200 μm thick, is composed of thin-walled parenchyma cells in the inner zone and thick-walled parenchyma in the outer zone. Resin canals, are elliptical in cross section, 120–140×350–500 μm in dimensions, and occur about midway between the inner and outer edges of the cortex (Fig. 3C, E).

The vascular trace to each bract-scale complex diverges from the vascular cylinder of the cone axis as a single thick strand that is open adaxially end C-shaped in cross section (Fig. 1A, B; Fig. 4A, B). A narrow gap in the vascular cylinder occurs in conjunction with trace departure. The diverging C-shaped trace branches from each adaxial and, supplying scale. The rest of the abaxial crescent-shaped trace goes into the bract (Fig. 1C; Fig. 4B, C). The strands are arranged in a ring as a whole, although the adaxial traces are fewer in number, and smaller in size than the abaxial traces (Fig. 1D, E; Fig. 4D).

Bract-scale complex. The bract-scale complex extends 6–9 mm out of the main axis. It consists of a basal stalk region and an upturned laminar region (Fig. 2C, D). The stalk is 3–6 mm long, 1 mm thick and projects from the cone axis at an adaxial angle of 80°–90° near the cone base and at an angle of 50°–60° near the cone apex. The laminar region is up to 6 mm wide and 2.5–4.0 mm thick. From the apex of the complex projects a small structure about 1 mm long that represents the bract tip (Fig. 2C). The fundamental tissue of basal part of the complex is composed only of sclerenchyma fibers, polygonal in cross section, 24–70 μm in diameter (Fig. 4C). In the upper laminar part of the complex the fibers become scattered among parenchyma cells (Fig. 2E). At the center of the complex, there are up to ten large resin canals arranged in a single horizontal row on the abaxial side of vascular strands of the bract, and four to six canals on the adaxial side of vascular strands of the scale (Fig. 1D–F; Fig. 4E).

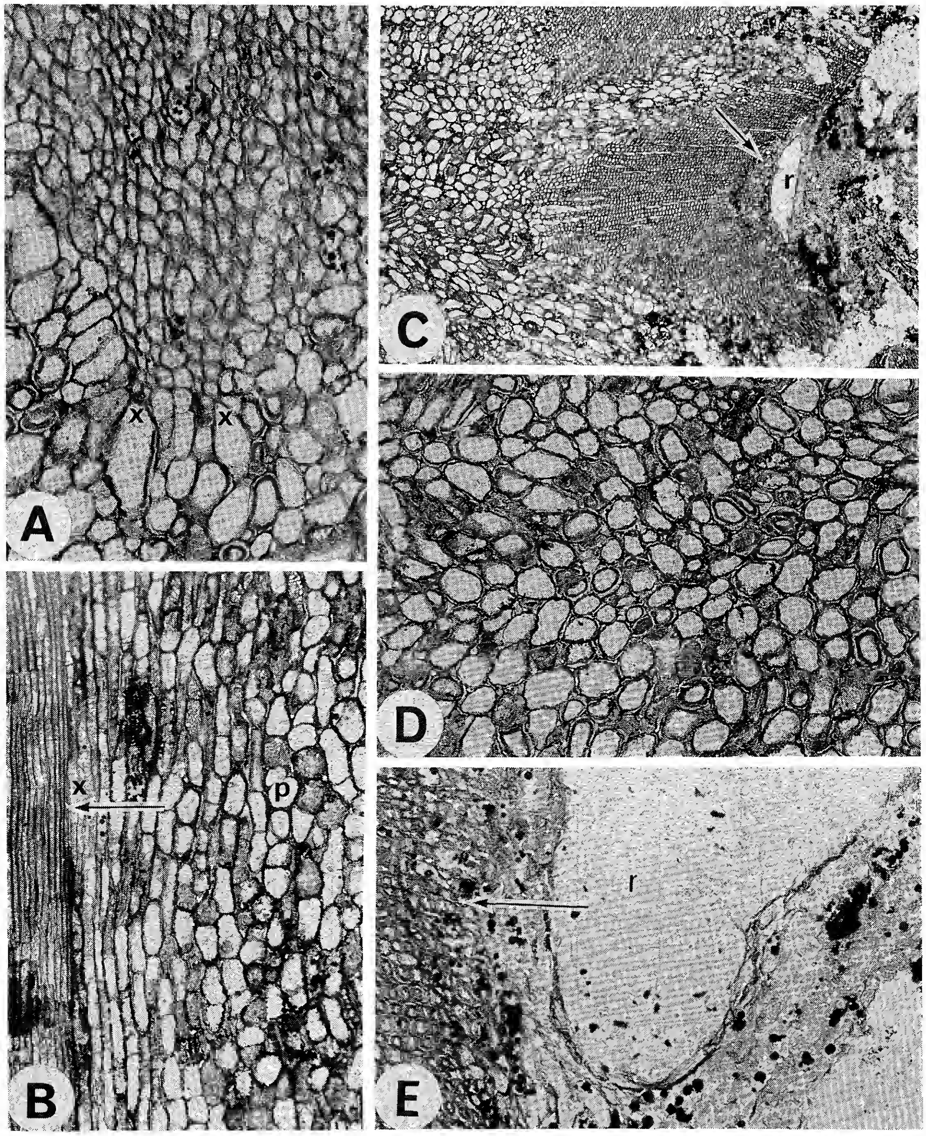

Fig. 3. *Yezosequoia shimanukii* sp. nov.
A: Cross section of cone axis, showing protoxylem and periphery of pith. B: Longitudinal section of cone axis, showing primary xylem and pith. Peripheral zone of the pith consists of elongate cells and inner part consists of polygonal cells in which thick-walled cells are included. C: Cross section of cone axis showing a part of vascular bundle consisting of primary and secondary xylem and phloem (arrow). D: Cross section of pith of cone axis, consisting of thin- and thick-walled cells. E: Cross section of cone axis, showing a part of secondary phloem (arrow) and inner cortex. p: pith. r: resin canal. x (arrow): protoxylem. A: ×136. B: ×68. C: ×27. D: ×136. E: ×136.

Epithelial cells of resin canals are not visible due to poor preservation of tissues. Distally, the stalk broadens to 2 mm wide and 2 mm thick and continues into the laminar zone. The bract trace branches, forming ten or more strands which remain close to one another and arranged in a horizontal row in the middle of the complex (Fig. 1F, G; Fig. 4D, E). The middle strand is the

largest. Scale vascular strands are four to six in number and also remain horizontally arranged adaxial to the bract strands (Fig. 1F, G; Fig. 4D, E). The parenchyma cells in the laminar part of the complex are rectangular with their longer axis parallel to that of the fibers and 31–80 μm in diameter and 40–100 μm long, while the fibers are 25–38 μm in diameter and up to 500–760 μm long with thick cell walls and very small cell lumens. The fibers have their longitudinal axes

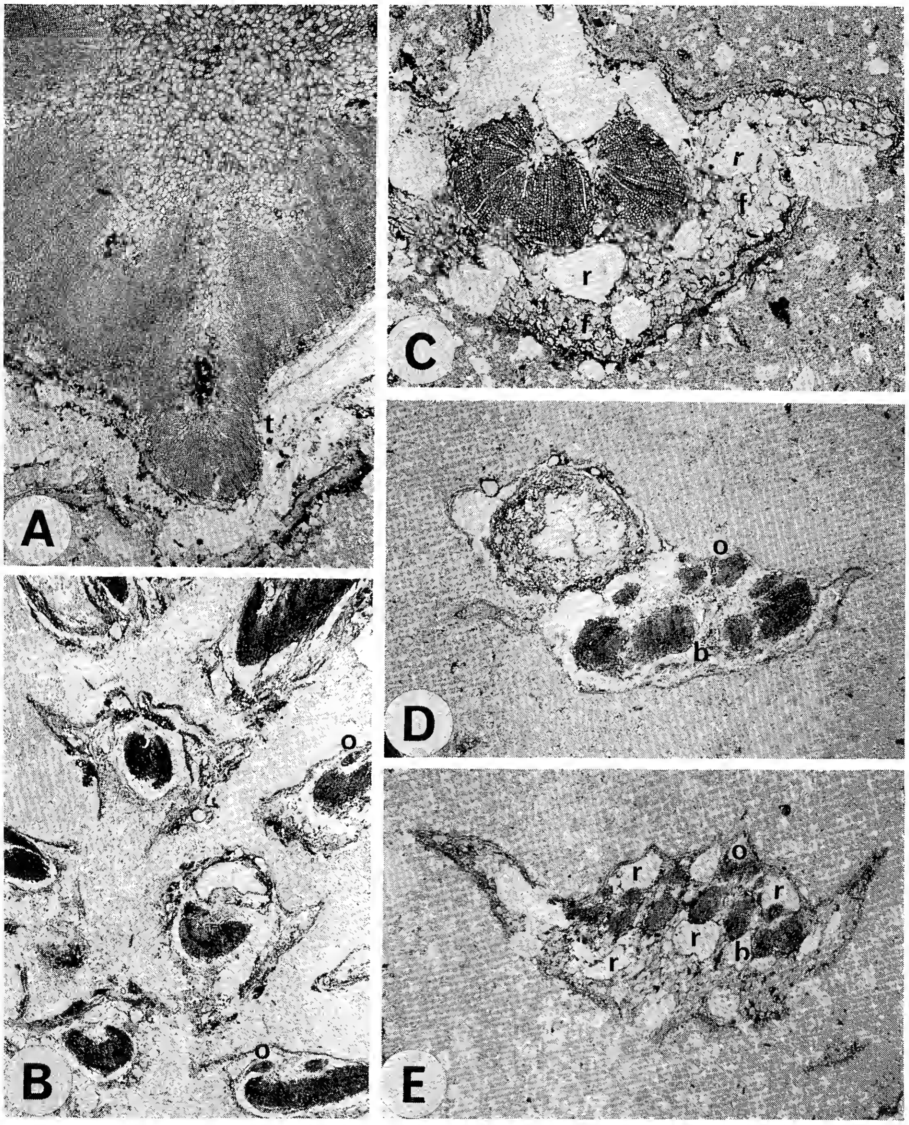

Fig. 4. *Yezosequoia shimanukii* sp. nov.
A: Cross section of a part of the vascular cylinder of the cone axis showing bract-scale complex trace (t). B: Cross sections showing basal portions of bract-scale complexes with c-shaped traces. C: Cross section of basal part of a bract-scale complex with vascular trace dividing into three strands. D: Cross section of median part of cone-scale complex with circularly arranged vascular strands; four upper strands are ovuliferous (o) and lower four are bracteal (b). E: Cross section of bract-scale complex, distal to that in D, showing two bands of vascular tissue, upper are scale (o) and lower are bract strands (b). b: bract strand, o: scale strand, r: resin canal. A: ×16. B: ×8. C: ×22. D: ×14. E: ×14.

parallel to that of the bract and mostly occur solitary but sometimes in clusters of two to four cells. Numerous resin canals occur in the distal part of the bract, being restricted to the ground tissue abaxial to the vascular strands (Fig. 1F–H; Fig. 4E; Fig. 5A).

The epidermis consists of a single layer of thick-walled cells that are about 14 μm in width and 34–67 μm long. Beneath this tissue is a hypodermis of one to three cell layers of thick-walled

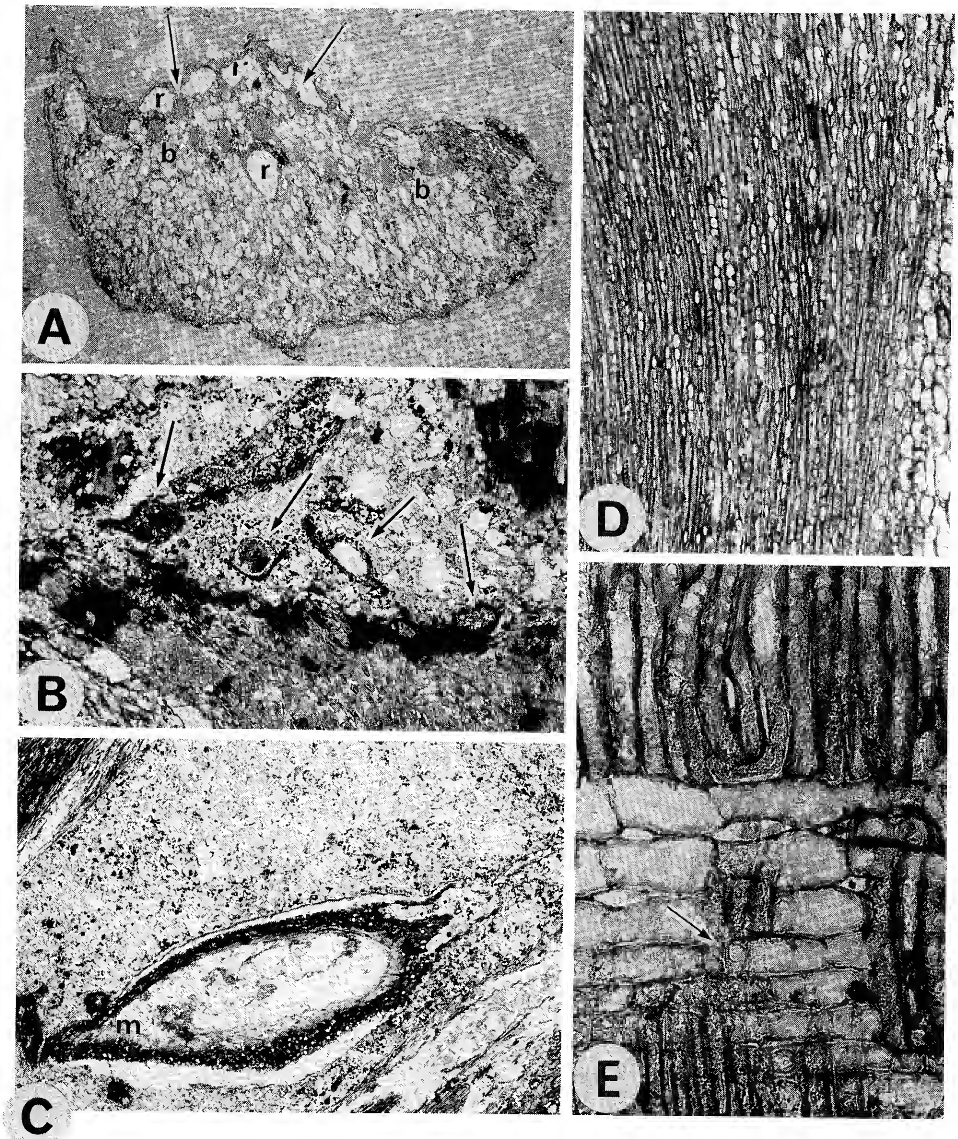

Fig. 5. *Yezosequoia shimanukii* sp. nov.
A: Cross section of cone-scale complex, distal to that in E of Fig. 4. Ovuliferous strands (arrows) are still visible. Bract strands (b) are arranged in a horizontal line. Resin canals (r) are located adaxial to scale strands and abaxial to bract strands. B: Cross section of bract-scale complex bearing four winged ovules (arrows). C: Longitudinal section of an ovule, micropyle (m) towards cone axis. D: Tangential section of the secondary xylem of cone axis. E: Radial section of the secondary xylem of cone axis, showing bordered pits on tracheids (upper side) and a single cross field pit (arrow). A: ×12. B: ×11. C: ×23. D: ×71. E: ×285.

fibers. These cells are 34–67 μm in diameter, 500–760 μm long and have cell walls that are 12–24 μm thick. The hypodermis tends to be thicker on the abaxial side of the bract than on the adaxial side (Fig. 4E; Fig. 5A).

Seeds. The actual attachment of the seeds to the scale is not visible in the available sections. Four ovules, however, are recognized on one bract-scale complex (Fig. 5B). Presumably, ovules are attached to the scale with their micropyles projecting toward the cone axis as in most modern Taxodiaceae (Fig. 2D; Fig. 5C). They are up to 1.2 mm thick and 2.4 mm long in longitudinal section (Fig. 2D). Seeds have narrow lateral wings.

Affinity. These cone specimens show the closest similarities to the Taxodiaceae in gross morphology, especially in having a peltate bract-scale complex consisting of large bract and small scale, which are completely fused with each other. Taxodiaceous cones are separable into four types depending on the morphology of bract-scale complexes, the size of scales and bracts, the orientation of the ovules and vasculature to the complex.

The first type represented by *Sciadopytis* has non-peltate bract-scale complex consisting of a large scale with inverted ovules and small bract. The complex is supplied with a single vascular bundle like those seen in pinaceous cones (Satake 1934).

The second type including *Cryptomeria, Glyptostrobus* and *Taxodium* have cuneiform or non-peltate bract-scale complexes (though peltate in *Taxodium*), somewhat small bracts, erect ovules and circular trace to bract-scale complexes, namely open type of vasculature (Satake 1934, La Pasha and Miller 1981).

Sequoia, Sequoiadendron and *Metasequoia* have peltate bract-scale complexes, equal sized scales and bracts, inverted ovules and circular trace to bract-scale complexes (Eames 1913, Hirmer 1936, La Pasha and Miller 1981).

Cunninghamia and *Taiwania* have tapering non-peltate bract-scale complexes, large bracts and reduced scales, with inverted ovules and terete traces to bract-scale complexes (Satake 1934).

Athrotaxis has wide ranges of variations in these characters and cannot be included in any of the above four morphological types. *Athrotaxis cupressoides* exhibits similar cone morphology and vasculature to both *Cryptomeria* and *Sequoia,* but it has a more reduced bract. *Athrotaxis selaginoides* shows the same morphology and vasculature as in cones of *Cunninghamia* (Eames 1913, Hirmer 1936). *Athrotaxis laxifolia* has an intermediate form between of *A. cupressoides* and *A. selaginoides* (Eames 1913, Hirmer 1936), and is sometimes considered as a hybrid between *A. cupressoides* and *A. selaginoides* (Dallimore and Jackson 1966).

Of the nine genera of the Taxodiaceae, peltate bract-scale complexes do not occur in *Cryptomeria, Taiwania, Cunninghamia,* one species of *Athrotaxis* (*A. selaginoides*), *Glyptostrobus* and *Sciadopitys.* On the other hand *Sequoia, Sequoiadendron, Taxodium, Metasequoia* and *Athrotaxis cupressoides* have peltate complexes (Dallimore and Jackson 1966). Our specimens are similar to the latter group in this respect. *Taxodium* has erect ovules on the complex, while our specimens have inverted ovules whose micropyles are directed toward the cone axis (Fig. 2C; Fig. 5C). *Metasequoia* has a decussate arrangement of the complexes around the cone axis, while our specimens exhibit helical arrangement. The new cones, therefore, resemble *Sequoia, Sequoiadendron* and *Athrotaxis cupressoides* in gross morphology.

Our specimens also have very similar cone morphology and vasculature to those of *A. laxifolia:* with cuneiform or somewhat peltate bract-scale complexes, small scales and large bracts and

C-shaped traces to bract-scale complexes (neither circular nor terete). Histological comparison were available between our specimens and *Sequoia sempervirens, Athrotaxis cupressoides* and *A. selaginoides* based on micropreparations loaned from Dr. C. N. Miller Jr. *Sequoia* was most similar to our specimens in having prominent fibers in the fundamental tissue of the bract-scale complex, and in shape of parenchyma cells in the fundamental tissue, which are rectangular with their longer axis parallel to that of the fibers. *Athrotaxis* species are clearly distinguishable from either our specimen or *Sequoia* in that they almost lack such fibers, and have parenchyma cells of irregular shape. *Sequoia,* however, is separable from our specimens in the form of first strand derived from the main axis.

Considering that variations in morphology of bract-scale complexes, in size of scales and bracts, and in form of traces to the bract-scale complexes occur in one genus *Athrotaxis,* it is difficult to attribute the new fossil cones to a particular extant genus or species using any of these characters. Critical character evaluation based on wider comparison of fossil and extant taxa of the Coniferophytes is needed to place the fossil at a certain point in the evolution of the Taxodiaceae.

There are about ten genera of petrified cones assignable to the Taxodiaceae from the Mesozoic. *Cunninghamiostrobus* includes two species, one from the Cretaceous of Hokkaido, Japan (Ogura 1930) and another from the Cretaceous of New Jersey, U.S.A. (Miller 1975). These have a close affinity to extant *Cunninghamia.*

Sphenolepis from the Jurassic of Belgium (Schenk 1871, Harris 1953) differs from our specimens in having horizontally arranged vascular strands in the complex as in *Cunninghamia* and complex traces exhibiting short straight bands in cross section. Moreover, *Sphenolepis* lacks fibers in the ground tissue of the complex (Harris 1953).

Elatides from the Upper Jurassic of Northern Europe (Harris 1953) and the Lower Cretaceous of Siberia and Spitzbergen (Heer 1876) does not show peltate structure of the complex. In addition, it has a horizontal arrangement of vascular bundles and ligule-like scale of the complex as in *Cunninghamia.*

Nephrostrobus from the Upper Cretaceous of New Jersey, U.S.A. (La Pasha and Miller 1981) has peltate bract-scale complexes, but differs from our specimen in having unique characters which are not seen in any extant or extinct genera of the Taxodiaceae. Vascular bundles in the complex of *Nephrostrobus* are arranged in adaxially concave reniform patterns. The most distinct feature is that the adaxial strand is the largest in the bundles.

Rhombostrobus from the same locality and horizon as *Nephrostrobus* (La Pasha and Miller 1981) is an incomplete specimen known as only tangential sections of the cone providing cross sections of the complexes. The complexes are not peltate but wedge-shaped structures and rhomboidal in shape in cross section. The vascular arrangement is not clear due to poor preservation. Resin canals, however, are arranged in a horizontal row as in *Cunninghamia.*

Athrotaxites from the Lower Cretaceous of British Columbia, Canada and Montana, U.S.A. (Miller and La Pasha 1983) has small cones, 18 mm × 12 mm consisting of about 20 bract-scale complexes which are wedge-shaped and bearing spine like projections. They most closely resemble *Athrotaxis cupressoides.*

Austrosequoia from the Upper Cretaceous of Queensland, Australia (Peters and Christophel 1978) has peltate bract-scale complexes without spine-like projections but with a medium transverse groove. The groove is similar to those seen in *Sequoia* and *Sequoiadendron.* Although the vascular arrangement of this genus has not been

described, it has been interpreted as having a close affinity to *Sequoia* and *Sequoiadendron* (Peters and Christophel 1978).

Our fossil cones are distinguishable from the Mesozoic cones mentioned above based on bract-scale complex architecture and internal anatomy. The new cones are, therefore, designated as a new genus of the Taxodiaceae and are supposed to have an affinities with *Sequoia* Group.

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要 旨

小平町川上の小平蘂川の河床，及び三笠市桂沢湖北岸の熊追沢から，嶋貫年男，中島勇の両氏がそれぞれ採集した球果は，卵型の楕円体で，20個以上の果鱗複合体が球果軸にらせん配列し，高さ29 mm，最大径25 mmに達する．果鱗複合体は完全に癒着した小さな種鱗と大きな苞鱗とからなり，全体としてほぼ盾形で，先端に刺状突起があるが，これは苞鱗の先端と見られる．果鱗複合体跡は横断面で向軸側に開口したC字形で，両端から向軸側に小さな維管束を分出し，全体としてさらに細分して上下二列に配列するようになる（図1，A－E）．向軸側の種鱗維管束の向軸側（外側）と，背軸側の苞鱗維管束の背軸側（外側）に樹脂道が並ぶ（図1，F，G）．胚珠は倒生で（図2，D）種鱗上に4個生じ種子には側方に翼がある（図5，B）．果鱗複合体の形態と維管束走行は*Athrotaxis luxifolia*とよく似ているが，基本組織の柔細胞が果鱗複合体の長軸方向に長い長方形であること，厚壁の繊維が多数ある点は*Sequoia sempervirens*に似ている．*Athrotaxis luxifolia*には繊維がほとんどなく，柔細胞は不規則な直径の多角形である．*Sequoia sempervirens*は果鱗複合体跡は横断面で環状である．*Sequoia*近縁のスギ科絶滅属と考えられ，*Yezosequoia*と命名した．